

Demography of Woody Plants in Relation to Fire: *Telopea speciosissima*

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Data on survival and reproduction within populations of *Telopea speciosissima* were collected over 4 years. These data were used in conjunction with an existing demographic model to predict population trends under regimes of frequent fire. The results indicate that recruitment will be absent when fire frequency is high (~ 5 year cycles) because young juvenile plants are not sufficiently developed to resprout. Under 10 year cycles of fire, recruitment may be sufficient to maintain stable populations if growth and maturation of juveniles is relatively rapid. Further studies of growth are needed to validate this prediction.

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INTRODUCTION

Research on the demography of woody plants in fire-prone, Australian vegetation has focussed on species which accumulate seeds in on-plant or soil storages (e.g. Auld 1987a; Bradstock 1990; Cowling *et al.* 1990). In some cases (Auld 1987a; Bradstock and O'Connell 1988; Bradstock 1990; Burgman and Lamont 1992) demographic information of this kind has been used in quantitative models to predict the population dynamics of species. Such methods have been used to draw conclusions about the persistence of populations when exposed to a range of fire regimes.

Among woody plant species that inhabit fire-prone environments, there are a variety of traits and syndromes of survival and reproduction (Kruger 1983). There is evidence that some longer-lived woody species may rely on rapid post-fire seed production rather than a long-lived seedbank in fire-prone habitats (e.g. Auld 1987b, 1990). Plants of the genus *Telopea* (waratahs) appear to possess reproductive characteristics keyed to fire. In *Telopea speciosissima*, a species with a distribution centred around the Sydney region of eastern Australia (Blomberry and Maloney 1992), a pronounced pulse of post-fire flowering has been described by Pyke (1983) and Whelan and Goldingay (1989). Seeds are apparently non-dormant, germinating readily upon wetting (Blomberry and Maloney 1992) and plants are also known to resprout following fire. In these respects the species exhibits life-history characteristics that are broadly similar to *Angophora hispida* (Auld 1987b, 1990), a common shrub in the Sydney area.

The aim of this paper was to collect demographic data for *T. speciosissima* and to use the data in a population model to investigate how well populations may persist under regimes of frequent fire. Emphasis was placed on frequent fire in this study because of the fire-induced flowering response that seems typical of the genus. Past management practices in some areas have been to burn waratah populations as often as possible to deliberately promote spectacular displays of post-fire flowering. This has resulted in the exposure of some populations to fires as often as every 4-5 years. Demographic studies of other woody species of plants (e.g. Bradstock 1990) predict that populations can decline under such regimes of frequent fire.

METHODS

The model developed by Bradstock (1990) for populations of serotinous resprouters can be used to estimate the number of fire tolerant juvenile plants (R_s) recruited per adult needed to maintain population density and structure.

$$R_s = \frac{(1-Sfa) + (Sfa \cdot (1-[Sua]^i))}{(Sfj \cdot (Suj)^n)} \quad (1)$$

where: Sua and Suj are the annual rates of survival of adults and juveniles respectively (unburnt conditions); Sfa and Sfj are the survival rates of adults and juveniles during fires; i is the interval between fires and n is the number of cycles of fire experienced by fire-tolerant juveniles (i.e. a parameter that reflects rate of growth) before maturation. Equation 1) effectively indicates the demand for recruitment. The adequacy of supply of individuals (R_s^*) and thus the likelihood that populations will remain stable in numbers can be estimated from

$$R_s^* = B \cdot E \cdot S_s \cdot S_{uj} \cdot S_{ufj} \quad (2)$$

where; B is the viable seedbank (number of viable seeds per adult); E is the proportion emerging as seedlings; S_s is the proportion of seedlings surviving to 3 years of age; S_{uj} is the proportion of young juveniles (plants > 3 years old) surviving until they experience their first fire; and S_{ufj} is the proportion of young juveniles that survive their first fire, thus becoming fire-tolerant juveniles. Equations 1) and 2) constitute a population model which assumes that seedling establishment is concentrated into a single post-fire period or event. The object of this study was to collect sufficient data to estimate these population parameters, so that solutions to the model could be explored. In particular, population stability was estimated under two scenarios of growth ($n = 1$ & 2 alternatively, high and low respectively; see equation 1) above) when subjected to a constant fire frequency (i) of 10 years. Within each growth scenario alternative simulations were performed to explore the sensitivity of predictions to variations in survival. The growth values were chosen to represent plausible rates of juvenile growth derived from subjective impressions during the study. Formal long-term estimates of growth in juveniles were prevented by a fire during the study (see below).

The study was done within the Brisbane Water National Park about 80 km north of Sydney. *Telopea speciosissima* is present there in a number of small populations situated in low open forest on deep yellow earths derived from laterite (Benson and Fallding 1981). The species is absent from neighbouring forests and woodlands situated on more sandy soils.

The methods used were broadly similar to those of previous demographic studies of woody plants in the Sydney region (Auld 1987ab; Auld *et al.* 1993; Bradstock and Myerscough 1988; Bradstock and O'Connell 1988). Observations were carried out over a six year period (1987–1993) within populations of differing fire history (time since last fire), to measure aspects of fruit production and rates of survival of adults, juveniles and young juveniles. Previous demographic studies of fire-prone resprouters (Bradstock and Myerscough 1988; Auld 1990) have identified the young juvenile life-stage (before plants are able to tolerate fires), as the most critical in the life-cycle. The minimum age of fire tolerance demarcates the effective upper limit to fire frequency above which no recruitment is possible. An experiment was performed to examine fire-survival in young juveniles.

Measurements of survival and fruit production were carried out in areas last burnt in 1976, 1980 and 1986 (Fig. 1). Two separate samples of plants were tagged in each fire

history class during early 1987. Within each site a random sample of 50–90 adjacent adult and juvenile plants was tagged. Height, number of stems, and position of lignotuber relative to the soil surface were measured on each individual. In the 1980a site large numbers of young juveniles were present, having established since 1984. A sample of 100 plants was tagged and monitored. Details of height, lignotuber exposure and diameter were recorded.

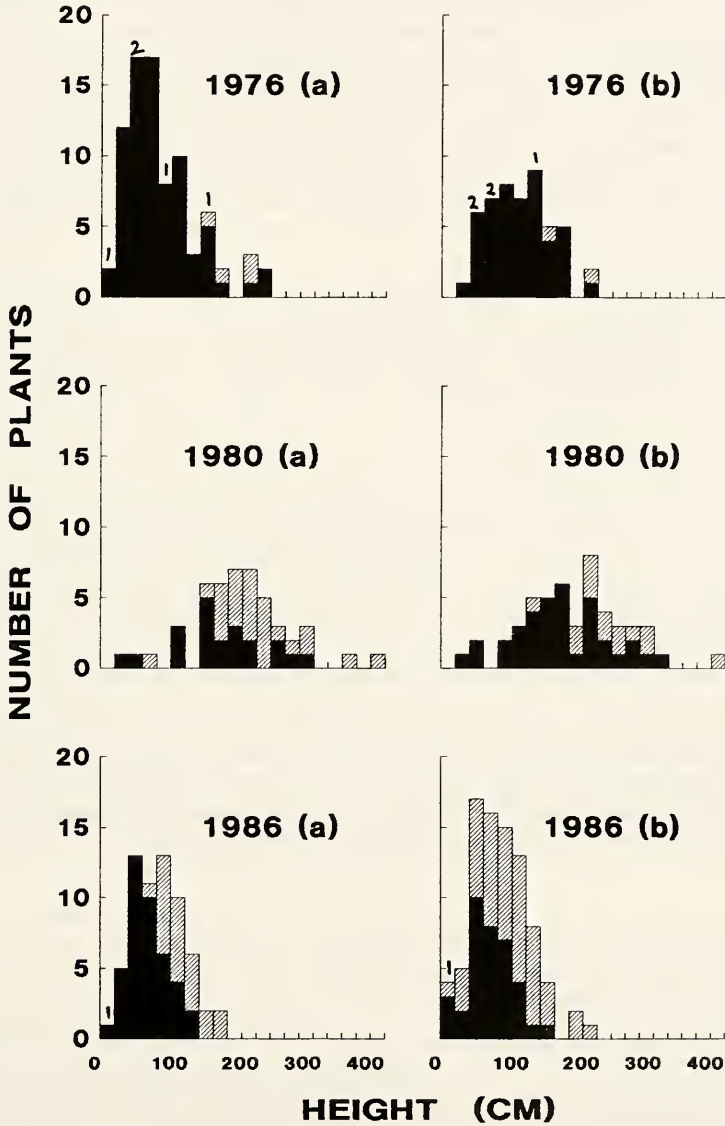


Fig. 1. Fruiting and survival as a function of plant size in *T. speciosissima* populations of different fire history. Numerals indicate number of deaths during the study in each size class, while hatching indicates numbers of plants which set fruits.

The tagged plants were revisited annually, and survival was checked along with flowering and fruiting in adults. All sites were burnt by an extensive wildfire on the 23–24/12/90. Fire behaviour on the 23/12/90 was extreme, resulting in total scorch or consumption of the forest canopy. Based on fuel consumption patterns the highest fire intensity was experienced in the 1976 and 1980 sites. There, some of the stems of live adults (2–3 cm thick) were completely consumed. Little ash remained in these sites and anecdotal information on rate of spread combined with likely fuel quantities (see Conroy 1993) indicated a maximum fire intensity of about 20000 kW/m within these sites.

Immediately after the fire, all sites were revisited and the tags checked. In most sites the tags had been placed on the branches of individuals. This posed a problem at some sites where the branches were consumed. Where possible the charred stumps of stems were located and re-tagged, with the assistance of pre-fire maps of locations of tagged plants. In some instances no plant remains could be found and tags were left where found. Some tags, particularly in one 1976 sample, were not found. Plants were re-sampled in subsequent years and survival monitored. Some unallocated tags were matched to plants following the commencement of resprouting. Care was taken to ensure that unallocated tags were re-matched to their original individuals. Post-fire survival was checked in late 1991 or 1992.

An experiment aimed at investigating fire tolerance of young juveniles was performed in 1988–89 at the 1980a site. Forty individuals were selected and randomly allocated in equal numbers to alternative treatments: stem severed or; stem severed plus burning. The treatments were performed in February 1988 and the plants were revisited at six monthly intervals thereafter. Prior to treatment, height, number of leaves and stems, lignotuber position and diameter were measured. Burning was carried out with a propane torch following removal of surrounding litter according to the method described in Bradstock and Myerscough (1988). This treatment was found to approximate the level of heating that would occur in a low intensity fire (about 500 kW/m; Bradstock and Myerscough 1988). The effects of treatments on survival were contrasted with survival of untreated plants monitored at the same site over the same time. Survival frequencies of treated and untreated plants were compared using a G test of independence (Zar 1974).

Seedling establishment rates were estimated in the 1986 sites by searching for seedlings in the area surrounding clusters of fecund adults, after seeds had been shed from freshly ripened fruits in 1989–90. The viable seed crop of these adults was estimated from fruit counts. Values for mean number of seeds per fruit were derived by harvesting forty fruits from the site in 1989 and counting the number of intact seeds in each fruit. Viability of seeds from this sample was tested in the laboratory. Four replicates of 25 seeds were placed on saturated filter paper within petri dishes for 8 weeks. Germinants were regularly scored and removed and the viability of remaining seeds was estimated using the tetrazolium test according to methods described in Bradstock (1990).

RESULTS

Survival

During the study, the plants that set fruit were of varied size (Fig. 1). Therefore for the purpose of describing survival, no attempt was made to distinguish between adults and juveniles. Few deaths were recorded among adults and juveniles before the 1990 fire (Fig. 1; Table 1). In contrast, survival was lower among young juveniles at the 1980a site over the same period (Table 1). Survival of the 1990 fire (Fig 1; Table 1) was highly varied within and between life-stages and between sites. Fire induced mortality was unrelated to size characteristics in adults and juveniles. The cutting/burning experiment performed on

young juveniles indicated low survival when burnt and cut (Table 2). Analysis indicated that cutting and burning significantly affected survival ($G = 35.05$, d.f. = 2, $p < 0.001$). There was a significant difference between burning and cutting treatments ($G = 5.88$, d.f. = 1, $p < 0.025$).

TABLE 1

Survival (Su - unburnt, Sf - burnt) of T. speciosissima plants from populations of varying fire history. See text for definition of survival rates and life-stages. Note removal of 29 young juvenile plants from the 1980a sample, post-fire, due to destruction of tags and disturbance of the site.

a) adults and juveniles

Site	No. initially tagged	No. of deaths pre-fire (1987-90)	Su	No. of fire-related deaths (1991-92)	Sf
1980a	42	0	1.0	1	0.98
1980b	49	0	1.0	1	0.98
1986a	80	5	0.94	3	0.96
1986b	73	0	1.0	4	0.95
1976a	63	0	1.0	2	0.97
1976b	50	4	0.92	8	0.83

b) young juveniles

Site	No. of plants	No. of pre-fire deaths (Sujj)			No. of fire-related deaths	Sfj
		1988	1989	1990		
1980a	97	8 (0.09)	8 (0.10)	2 (0.03)	39	0.22

TABLE 2

Survival of young juveniles subjected to cutting and burning treatments.

Survival	Treatments		
	Cut and burnt	Cut only	Control
Alive	5	13	73
Dead	15	8	8

Fruit production

Fruits were mostly produced in the more recently burnt sites (Fig. 2). In these sites, the size of annual crops declined prior to the 1990 fire (Fig. 2). Fruiting was restricted to a relatively small number of plants except in the 1980a site but, as noted, was spread among plants of varied size (Fig. 1). The first post-fire fruit crop in the 1986 sites was produced in 1988 after which fruiting increased and declined.

Seedling establishment and survival

There were 12.6 ± 0.7 intact seeds per fruit (mean \pm se). The viable proportion of intact seeds was 0.82 ± 0.10 . Estimates of seedling establishment in the 1986 sites varied considerably between different parent plants (Table 3). All seedlings tagged in 1990 were subsequently killed by the fire in these sites.

Estimation of recruitment under different fire regimes

Juvenile recruitment was estimated for the two growth scenarios (see above) and two survival scenarios based on results in Table 1 (high survival, Suj & Sua = 0.995, Sfj & Sfa = 0.97; low survival, Suj & Sua = 0.92, Sfj & Sfa = 0.80). Values of juvenile recruitment (Rs, derived from equation 1) varied over a hundredfold range according to the estimates of growth used (Table 4). Recruitment estimates overall, however, were less sensitive to variations in growth than survival.

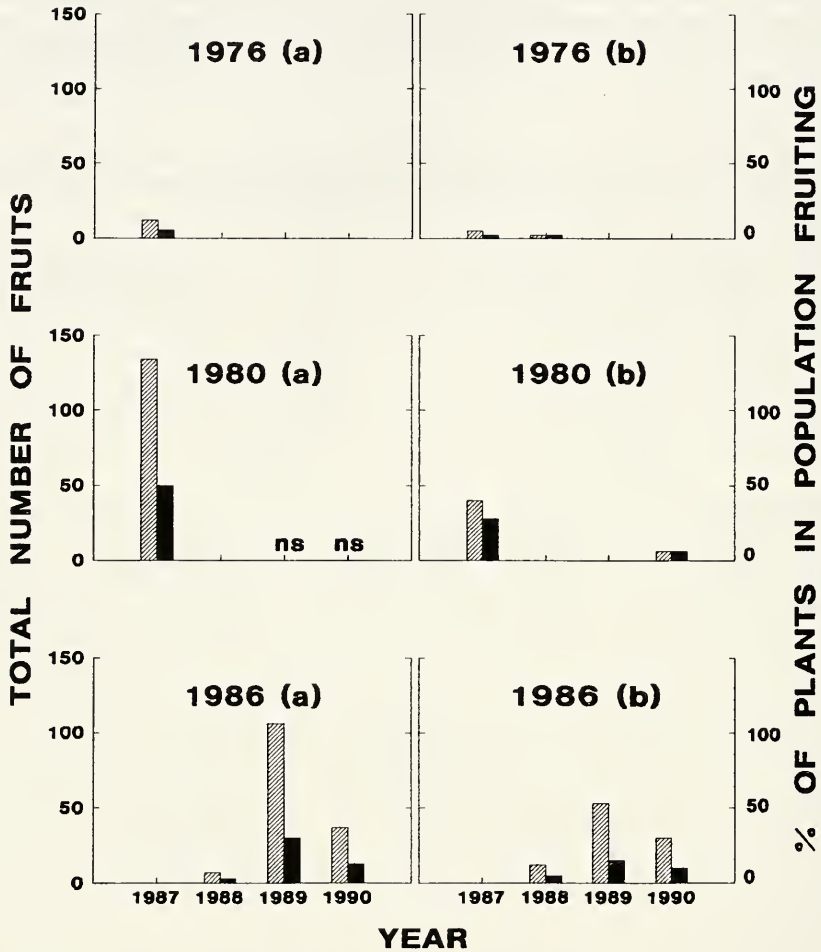


Fig. 2 Fecundity of *T. speciosissima* plants from populations of different fire history. Hatched bars indicate total fruit numbers per sample and solid bars indicate proportion of each sample that set fruits. Site 1980a not sampled in 1989-90.

TABLE 3
Establishment of *T. speciosissima* seedlings three years after fire in groups of adjacent adults, as a proportion of the intact viable seedbank (E)

Site	No. of adults in group	Total intact fruits	No. of seedlings	E
1986a	4	10	9	0.087
	4	12	6	0.049
	3	3	5	0.194
	3	6	3	0.048
1986b	3	36	29	0.078
	2	2	4	0.190
	3	13	28	0.210
	2	12	8	0.065
	1	12	1	0.008

TABLE 4
Scenarios of juvenile recruitment (Rs) necessary for a stable population, as a function of different values of growth and survival parameters (see text for definitions and values)

Growth	Survival	
	High	Low
High	0.091	5.41
Low	0.099	15.56

DISCUSSION

Effects of fire regimes

Based mainly on the survival of young juveniles in the burning/cutting experiment and the 1990 fire (Tables 1 and 2), it can be concluded that sustained high frequency fire (<10 year cycle) will cause populations to decline. At 8–10 years postfire <25% of young juveniles are fire tolerant: it could be expected that survival would be lower at an earlier age, because lignotubers would be less well developed. For example, the initial cohort of newly emerged seedlings in the 1986 sites were killed by fire in 1990. Therefore zero recruitment and a decline in density would be expected under a 4–5 year cycle of fire.

The estimates of juvenile recruitment, derived from equation 1), can be used to give a more detailed indication of population trends under a 10 year fire cycle. In order to do this, some indication of the likely supply of young juveniles (R_s^*) is needed based on seedbank, establishment and survival of young juveniles as specified in equation 2). Assuming half of emergent seedlings ($S_s = 0.5$, equation 2)) survive to 3 years of age (the transition age to the young juvenile phase; Bradstock 1990), equation 2) can be solved using estimates of the other parameters derived from the study (i.e. $S_{uj} = 0.93$ per annum; $S_{fj} = 0.22$; $E = 0.1$) for a cohort of seedlings emergent three years after fire. The seedling survival value of 0.5 is intermediate within the range found for other co-habiting proteaceous shrubs in the study area (Bradstock 1990; Bradstock and O'Connell 1988).

These values give an estimate for supply of young juveniles of $R_s^* = 0.008.B$ (where B is the viable seedbank, equation 2)). The level of seedbank per adult (B) necessary to meet the recruitment scenarios in Table 4 would lie between the extremes of 1 or 1.1 (growth parameter $n=1$; high or low survival scenario, Table 4) to 61.6 or 176.8 (growth parameter $n=2$; high or low survival) intact fruits per adult, assuming that there is a mean of 11 viable, intact seeds per fruit (see above).

It is apparent from data on post-fire fruiting in the 1986 sites that there would be adequate fruits and seeds to meet the high but not the low growth scenario (Fig. 2). Even taking into account fruit crops in the first and third year of post-fire flowering (not accounted for in the above calculations) in these sites, it is evident that there would be insufficient seedbank to maintain populations under the slower growth scenario. Fruiting of an order of magnitude greater than that measured would be necessary, an unlikely occurrence given that natural fruit production and seed set found in a study of a population south of Wollongong (Whelan and Goldingay 1989) were similar to that reported here.

Either an increase or decrease in seedling survival would not substantially alter these conclusions. If, for example, seedling survival was substantially lower ($S_s=0.10$) about 5 times more seedbank would be required for populations to be maintained (low growth scenario): i.e. each adult would have to produce a total of about 5 fruits in total from post-fire flowering. This is about the level of fruiting sustained in the 1986 populations after fire (Fig. 2). An increase in survival ($S_s=0.90$) would approximately halve the amount of seedbank required for population maintenance. This would be insufficient to

match the level of seedbank required under the low growth scenario.

Population stability may be possible under a fixed fire 10 year cycle but a definite conclusion will require further work on juvenile growth and maturation rates. Data were not available to estimate the seedling survival parameter, mainly because the cohort of emergents tagged in 1990 (1986 sites) were eliminated by the 1990 fire.

Implications for fire management

Acquisition of growth data would provide a suitable basis for further development of the model used here to explore extinction risk as a function of fire regimes in the manner described by Burgman *et al.* (1993). A version of the model predicting population extinction risk or viability would provide the most appropriate vehicle for exploring and comparing fire management scenarios. It would also provide a more appropriate means of exploring the outcome of stochastic variations in population parameters.

In the absence of such a model, a number of general conclusions can be drawn concerning management of fire and the maintenance of *Telopea* populations in the study area. Without data on juvenile growth it could be concluded that a conservative management aim would be to avoid sustained periods (>5 cycles) of high frequency fire (interval between fire <10 years). Occasional longer intervals between fire will provide a window of opportunity for effective recruitment of juveniles (Bradstock 1990). In this respect the population response to fire and the fire management objectives for conservation of waratah populations are broadly similar to other woody species capable of resprouting in the Sydney area (Bradstock 1990, Auld *et al.* 1993).

The past management strategy of deliberate high frequency burning to promote displays of flowering would not be sustainable in the long-term. Coupled with the problem of flower picking in some sites adjacent to roads (e.g. 1976 and 1986 sites) and the consequent reduction in seedbank and recruitment, such a management strategy could result in the depletion of populations. A more appropriate scenario for management is to allow the frequency of fire to vary in the longer term (Bradstock *et al.* 1995). Given that some of the populations monitored in this study (1986 sites) have experienced four fires in the period 1976–90, some thought needs to be given as to how a variable regime can be achieved in practice.

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